

# A productivity-based explanation for woodland bird declines: poorer soils yield less food

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**Abstract.** The decline of woodland birds in southern Australia has motivated considerable research, identifying which species, habitats and regions are most affected, but the mechanisms driving these declines remain unclear. Applying findings from plant ecology, hydrology and soil science, I evaluate how availability of water and nutrients has been altered by agricultural development and how those changes have affected woodland food webs. Selective clearing of woodlands on fertile soils and overgrazing of remaining native vegetation have lowered productivity, whereas the storage of water has shifted from within the soil to surface reservoirs. I suggest that these changes have had a profound impact on below-ground decomposer communities, leading to fewer ground-dwelling invertebrate prey and reduced insectivore numbers. This productivity-based hypothesis is congruent with many previous findings, explaining the susceptibility of ground-foraging insectivores to changing land-use (via nutritional limitation), the sensitivity of southern woodlands (via summer drought stress), and the decreased resilience of eucalypt woodlands (via lower litter-fall and greater sensitivity to eutrophication). I detail six testable predictions extending beyond birds to microbial communities, plants, and other woodland-dependent animals. Finally, I explore the implications of this hypothesis, highlighting the value of remnant habitat on productive land to the long-term persistence of woodland bird populations.

**Additional keywords:** declining woodland birds, eutrophication, farmland, food limitation, habitat fragmentation, insectivore, nectarivore.

## Introduction

Woodland birds are in serious trouble. Previously widespread species are now restricted, formerly abundant species are increasingly scarce and local extinctions have become commonplace. Most researchers documenting these patterns have been cautious not to extrapolate beyond their particular study area but, taken collectively, there is cause for genuine concern about the continued viability of woodland bird assemblages in many regions (Mac Nally *et al.* 2009). The loss of woodland birds from landscapes dominated by production agriculture have been recorded in southern Australia (Ford *et al.* 2001), Britain (Fuller *et al.* 2007; Hewson *et al.* 2007), western Europe (Donald *et al.* 2001) and North America (Robinson and Wilcove 1994; Murphy 2003), with declines of woodland birds now recognised as a global conservation priority (BirdLife International 2008).

The issue of declining woodland birds in Australia has motivated considerable research to quantify the nature and extent of the issue, conducted at scales ranging from hand-held quadrats to the entire continent (Ford 2011). These studies have used various methods to address many specific questions, but the logical basis of these approaches is comparable – what can we learn from studying current occurrence patterns of woodland birds? This top-down, taxon-specific work is essential to describe patterns, but cannot reveal the processes driving them. As such, there is now a large (and growing) body of evidence supporting a set of increasingly alarming patterns, but little progress in identifying the underlying mechanisms.

The purpose of this contribution is not to synthesise previous studies, search for hitherto overlooked traits of declining species nor evaluate how well existing hypotheses explain these pervasive declines. Rather, I take a different tack, and start with two of the raw materials all organisms need to survive – water and nutrients – and consider how their availability has changed in the woodlands of southern Australia since European settlement. As well as avian ecologists, these woodlands have been the subject of considerable research by plant ecologists, and the grazing and cropping landscapes that have replaced them have been studied extensively by soil biologists and hydrologists, generating information on how water and nutrient flows vary across space and through time (Ludwig *et al.* 1997; Tongway *et al.* 2003). By considering processes including fragmentation, grazing and habitat degradation using this common currency, I evaluate how the foundation of woodland food webs has changed since European settlement. I introduce and develop the thesis that fundamental changes in nutrient inputs and hydrology associated with land clearing and production agriculture have caused physical, chemical and biological changes to woodland soils, driving reductions in the abundance of soil- and litter-dwelling invertebrates – a major food source for many woodland birds. I revisit empirical studies of woodland birds and re-evaluate their findings in the light of this productivity-based hypothesis, demonstrating consistently close congruence. Rather than being restricted to insectivorous birds, the hypothesis also explains observed changes in other groups of animals and plants, conforming to the unified

diversity-productivity relationship (Huston 1979, 1994). Finally, I highlight emergent questions and articulate six testable predictions to guide further research and inform on-ground management to arrest further declines.

### Declining woodland birds

Given the proportion of vegetation cleared, the number of introduced predators and the extensive degradation of remaining habitat (Garnett 1992; Recher 1999), it is hardly surprising that woodland-dependent biota have undergone severe declines. Yet, not all woodland habitats have been equally affected; not all regions are involved; not all woodland bird species have declined (Reid 1999; Antos and Bennett 2006). It is this lack of uniformity that has confounded previous workers and refuted many other-wise sound explanations. I begin by defining the scope of the issue – addressing the who, what, where and when questions from existing studies of woodland birds. Having distilled the current understanding of the issue, I then consider the question of why – drawing on other studies of woodlands and focussing on the biotic and abiotic processes affecting productivity.

#### Who? Identifying which species are involved

Reid (1999) initially compiled a list of 20 woodland bird species that have declined in the sheep–wheat belt of New South Wales. These species were formerly common, widespread species characteristic of woodland habitats throughout the region that had undergone dramatic and ongoing declines, as distinct from species formally listed as threatened, vulnerable or endangered (Garnett 1992). As data from elsewhere emerged, this list of

‘declining woodland birds’ was expanded to include additional species and applied to south-eastern or southern Australia in general. In this contribution, I include all 26 of these species (Table 1) while noting that many other species of bird occurring in these woodlands have not undergone declines.

Patterns of occurrence, movement, foraging and reproduction of many of these species have been studied at a variety of scales in multiple habitat types (Ford *et al.* 2001; Ford 2011), and several generalities have emerged regarding the ecological traits of those bird species that have undergone declines. Those species that are resident, small-bodied, ground-foraging and insectivorous are more likely to have declined than otherwise similar species (both ecologically and evolutionarily; Reid 1999). Comparisons of this group with other woodland birds have found no other consistent differences in life history, with comparable reproductive rates, nest locations and distributional ranges (Ford *et al.* 2001).

#### What? Defining the ‘declining woodland birds’ issue

The term has been used to describe multiple patterns, including reductions in reporting rate, relative abundance, distributional range and reproductive output, as well as changes in overall species richness at site, patch, landscape and regional scales. Although these patterns are interrelated, the accuracy of available data varies. Thus, changes in distributional range are clearly documented and congruent across many studies, but changes in relative abundance are more variable and the estimates more sensitive to sampling methods. For the purposes of this

**Table 1.** List of the 26 species considered to be declining woodland birds (after Reid 1999; Robinson and Traill 1996) with principal diet and dominant foraging substrate

Name	English name	Principal diet	Substrate(s)
<i>Dromaius novaehollandiae</i>	Emu	Fruit, seeds, arthropods	Ground
<i>Eurostodopus argus</i>	Spotted Nightjar	Arthropods	Ground, air
<i>Lophoictinia isura</i>	Square-tailed Kite	Vertebrates, arthropods	Ground, foliage
<i>Burhinus grallarius</i>	Bush stone-curlew	Arthropods, vertebrates	Ground
<i>Turnix varius</i>	Painted Button-quail	Seeds, arthropods	Ground
<i>Lathamus discolor</i>	Swift Parrot	Nectar, arthropods	Foliage
<i>Climacteris affinis</i>	White-browed Treecreeper	Arthropods	Bark, ground
<i>Climacteris picumnus</i>	Brown Treecreeper	Arthropods	Bark, ground
<i>Chthonicola sagittata</i>	Speckled Warbler	Arthropods	Ground
<i>Acanthiza uropygialis</i>	Chestnut-rumped Thornbill	Arthropods	Ground
<i>Aphelocephala leucopsis</i>	Southern Whiteface	Arthropods	Ground
<i>Anthochaera phrygia</i>	Regent Honeyeater	Nectar, arthropods	Foliage
<i>Pomatostomus temporalis</i>	Grey-crowned Babbler	Arthropods	Ground
<i>Pomatostomus superciliosus</i>	White-browed Babbler	Arthropods	Ground
<i>Daphoenositta chrysoptera</i>	Varied Sittella	Arthropods	Bark
<i>Falcunculus frontatus</i>	Crested Shrike-tit	Arthropods	Bark, foliage
<i>Pachycephala rufiventris</i>	Rufous Whistler	Arthropods	Bark, foliage
<i>Oreoica gutturalis</i>	Crested Bellbird	Arthropods	Ground
<i>Artamus superciliosus</i>	White-browed Woodswallow	Arthropods	Air
<i>Artamus cyanopterus</i>	Dusky Woodswallow	Arthropods	Air
<i>Myiagra inquieta</i>	Restless Flycatcher	Arthropods	Ground, air
<i>Microeca fascinans</i>	Jacky Winter	Arthropods	Ground
<i>Petroica goodenovii</i>	Red-capped Robin	Arthropods	Ground
<i>Melanodryas cucullata</i>	Hooded Robin	Arthropods	Ground
<i>Eopsaltria australis</i>	Eastern Yellow Robin	Arthropods	Ground
<i>Stagonopleura guttata</i>	Diamond Firetail	Seeds	Ground

contribution, I define the issue of declining woodland birds as follows:

‘Declining woodland birds are woodland-dependent species that have undergone widespread reductions in abundance and occurrence in southern Australia, reflected in diminishing population sizes and shrinking distributional ranges – especially in the southern and eastern parts of the region.’

#### *Where? Establishing the extent of declines*

This phenomenon has been studied principally in temperate eucalypt woodlands within agricultural landscapes in south-eastern Australia (both grazing and cropping), with comparable findings emerging from research in remnant eucalypt woodlands in southern Western Australia (Recher 1999). There are many other woodland types in southern Australia, but studies of birds occurring in these habitats have not detected the same declines (but see Woinarski *et al.* 2006 for comparable patterns noted in remnant Brigalow (*Acacia harpophylla*) woodlands in central Queensland). Research in woodlands dominated by species of *Acacia*, *Casuarina*–*Allocasuarina* and *Callitris* in southern Australia have documented far more intact communities of woodland birds (Leach and Recher 1993; Watson *et al.* 2000; Major *et al.* 2001; Antos and Bennett 2005; Oliver and Parker 2006) and many of the species of concern still occur in reasonable numbers in these other woodland types (Antos and Bennett 2005; Maron *et al.* 2005; Bowen *et al.* 2009). Hence, the phenomenon of declining woodland birds may, at present, be predominantly restricted to eucalypt-dominated temperate woodlands.

There are also regional differences, with declines largely reported from southern woodlands – specifically those woodlands in regions with winter rainfall. Woodlands located in summer rainfall regions to the north and the semiarid zone inland of the sheep–wheat belt have been subjected to similar historical changes and ongoing threats, but current data indicate that their bird assemblages have not undergone the same declines as their southern counterparts (Garnett 1992; Leach and Recher 1993; Bowen *et al.* 2009; but see Woinarski *et al.* 2006).

#### *When? Describing the historical basis of declines*

Declines in woodland birds were noted throughout the last century, but most reports were confined to particular districts or single localities. Three contemporaneous but independent papers (Goldney and Bowie 1990; Recher and Lim 1990; Robinson 1991) synthesised this information, calling attention to the generality of the signal emerging from these disparate findings. Subsequent work by Garnett (1992) and Reid (1999) described these declines in more detail, compiling qualitative and quantitative information on the species and regions involved. Declines were frequently reported in the 1960s–70s and, although there were earlier reports for some species, widespread local extinctions in woodland birds are generally considered to have occurred in the last 50 years, becoming increasingly pronounced in the last 20 (Robinson and Traill 1996; Traill *et al.* 1996; Recher 1999; Ford *et al.* 2001). This is not to say that changes in abundance and distribution were not occurring earlier, nor that the avifauna of

other habitats elsewhere was stable. Further details on the history and tempo of changes in woodland bird assemblages are not available, given the lack of long-term bird population survey data to complement changes in vegetation structure, but one pattern that emerges from these historical accounts is the coincidence of local extinctions with severe droughts (Reid 1999). The impact of drought (especially related to the El Niño–Southern Oscillation) on bird populations has been invoked by several authors (Woinarski *et al.* 2006; Mac Nally *et al.* 2009) and may exacerbate further the effects of changing land-use.

#### **Availability of nutrients and water in woodlands**

The woodlands of southern Australia have been cleared and fragmented, replaced by extensive monocultures of exotic annuals used for production agriculture and bisected by roads, fences, irrigation channels and easements for pipelines and powerlines (Yates and Hobbs 1997; Hobbs and Yates 2000). Remaining woodlands are now used for grazing, firewood collection and other extractive industries; they have been invaded by exotic plants and animals; and fires and floods have decreased in frequency (Recher and Lim 1990; McIntyre and Lavorel 1994). Instead of cataloguing the effects of these threats to woodland birds individually, I consider their combined effects in terms of nutrient inputs and availability of water to explore how the foundation of woodland food webs has changed.

Initial clearing and subsequent fragmentation of woodlands did not occur uniformly throughout southern Australia. Early land clearance was focussed around productive soils and reliable access to water and progressive conversion of woodlands to pasture and cropland was similarly non-random, preferentially clearing woodland from riparian zones, valley floors and floodplains (Recher and Lim 1990; Robinson and Traill 1996; Prober *et al.* 2002). Thus, woodland remnants are not representative of their former extent (Hobbs *et al.* 1993), but are disproportionately located on ridgetops, rocky hillsides and other parts of the landscape with soils poorly suited to production agriculture (an extension of the ‘worthless lands’ thesis of Runte 1979). Accordingly, I suggest that most remaining woodland was originally marginal habitat for many woodland-dependent species (after Prober and Thiele 1995).

Upon conversion from woodland-dominated landscapes to country suitable for cropping and livestock production, the distribution of water was dramatically modified. The original ephemeral creeks, gilgai and intermittent chains of ponds were replaced by a multitude of small dams – surface water concentrated spatially and available more permanently throughout the year (James *et al.* 1999). In addition to domestic stock, these fixed watering points also favour other grazing animals (native and exotic), intensifying the effects of grazing on surrounding vegetation (Ludwig *et al.* 1997). With increased grazing pressure, understorey communities changed as palatable species (especially legumes and other forbs) declined and deep-rooted perennial tussock grasses became successively replaced by annuals (primarily exotic species; McIntyre and Lavorel 1994; Landsberg and Crowley 2004). These changes decreased the amount of organic matter held within the soil and subsoil of woodlands, simplifying soil structure and decreasing water-holding capacity dramatically (Tongway *et al.* 2003, and refer-

ences therein). Overgrazing and associated trampling by ungulates reduced ground cover and disturbed cryptogamic and microbiotic crusts (thin layers comprising various lichens, mosses, liverworts, cyanobacteria and fungi in the top layer of the soil; Eldridge and Greene 1994) leading to soil compaction and decreased water infiltration, as well as losses of topsoil through erosion (Fanning 1994; Ludwig *et al.* 1997). Research from the New England Tableland has revealed how drastic these effects could be, documenting a fifty-fold increase in erosion rates after sheep grazing began in the 1830s (Gale and Haworth 2005). Moreover, they calculated that the soil lost in the first 25 years represented 85% of the total loss of soil since European contact (Gale and Haworth 2005). These landscape- and patch-scale effects were exacerbated by reductions in within-patch heterogeneity via removal of coarse woody debris from remaining woodlands, which is known to slow rates of waterflow and aid in infiltration, litter accumulation and microclimate amelioration at smaller scales (McIvor 2002). During the same period, many medium-sized fossorial marsupials (including bandicoots *Perameles* and *Isoodon* spp., bettongs *Bettongia* spp., and potoroos *Potorous* spp.) considered to perform critical roles in microtillage and dispersing large seeds and mycorrhizal fungi (Noble *et al.* 2007, and references therein) became regionally extinct (Dickman *et al.* 1993), further simplifying woodland soils and decreasing their resilience to further change in land-use. Finally, increased insolation and penetration of wind associated with the increased proportion of cleared canopies further desiccated woodland understoreys (see Murcia 1995; Didham 1997), increasing losses of litter and soil to adjacent (often down-slope) cleared land.

In terms of nutrients, livestock grazing led to greater concentration of nitrogen, magnesium and other animal-derived elements, especially in ridge-top remnants and beneath isolated paddock trees (Hilder and Mottershead 1963; Taylor *et al.* 1984). Increasing use of fertilisers in pastures and croplands increased levels of phosphorous in adjacent woodlands via surface runoff and spray drift (Yates and Hobbs 1997; Duncan *et al.* 2008). In some areas, the use of irrigation raised water-tables, increasing inputs of potassium, calcium and other cations into the soil (Hobbs and Yates 2000). Finally, the replacement of an understorey composed primarily of deep-rooted perennials with one dominated by shallow-rooted annuals led to a shift from low-level nitrate availability year-round to peaks in otherwise low availability, associated with growth cycles of exotic annuals (McIntyre and Lavorel 1994; Prober *et al.* 2002; Clarke 2003).

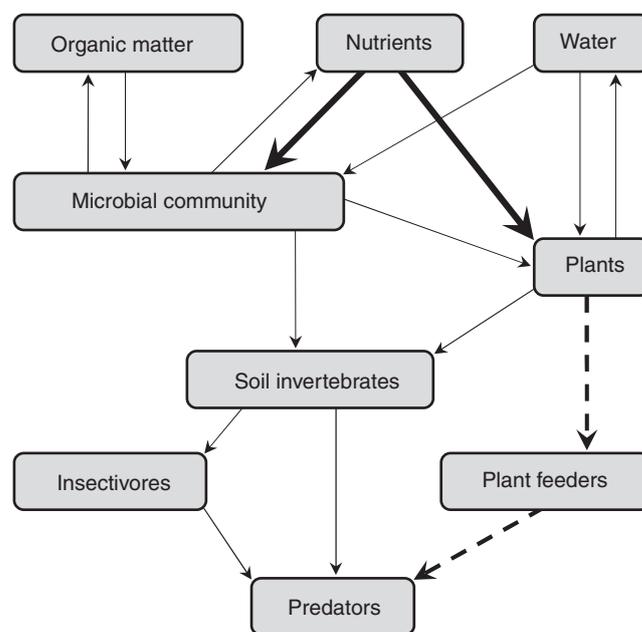
In sum, selective clearing of woodlands and intensification of land-use in remaining habitats has changed overall soil properties: organic matter and water-content have both decreased whereas availability and homogeneity of inorganic nutrients have increased. In addition to affecting plants, these changes have profound implications for the composition and function of decomposer communities, further affecting the availability of nutrients within woodlands. This below-ground biota is dominated (in terms of both diversity and biomass) by bacteria and fungi, the biological activity and functional diversity of which are largely determined by soil properties and nutrient inputs (Bardgett 2005). As well as determining the rate of decomposition and soil formation, microbial communities affect the

structure and composition of other soil biota that feed on them (King and Hutchinson 1983) thereby driving changes throughout the entire food web (Cole and Bardgett 2002).

### The productivity-based hypothesis for declining woodland birds

That:

‘The selective clearing of woodlands on more productive soils and degradation of remaining woodlands has driven reductions in the biomass of decomposer communities in the soil and litter, thereby reducing the food resources available to ground-feeding insectivores’ (Fig. 1).



**Fig. 1.** Energy flow through a typical southern Australian woodland. In this simplified diagram, narrow arrows depict pathways that have decreased since European settlement, thick arrows depict pathways that have increased, and dashed arrows represent pathways that have remained unchanged. Given disproportionate clearing of habitat on the more productive soils, most remaining woodland occurs on ridges, rocky slopes and other low productivity land forms – marginal habitat for most woodland-dependent species. The amount of organic matter in the soil of these remnants is lower, exacerbated by the shift in woodland understoreys from deep-rooted perennials to exotic annuals. Livestock and fertiliser drift increased flows of macronutrients, driving simplification of microbial communities under these eutrophic conditions, leading to less available food for below-ground communities and litter-dwelling invertebrates. Water infiltration decreased, running off compacted soils into surface impoundments, leading to more pronounced seasonal drought stress, especially in winter rainfall regions where the growing season has effectively shortened. Although reduced water and organic inputs are partly compensated by increased nutrients (energy flow from plants depicted as unchanged), there has been a shift within plant feeders from nectarivores to sap-feeders. With less invertebrate prey available, the number of insectivores that can be supported within a woodland decreases. Coupled with a reduction in larger soil-dwelling invertebrates, the number of predators is also expected to decrease, as they need to travel further to acquire the same nutritional resources.

In addition to affecting survivorship directly via foraging behaviour, movements and body condition, this reduction in available prey would constrain reproductive output, leading to reduced recruitment to subpopulations at local and regional scales. The effects of agricultural intensification on the structural, chemical and biological properties of soil have been studied extensively and, although scant research has been conducted within remnant vegetation, many studies have quantified these effects in the production landscapes that surround them. By drawing on existing studies and applying food-web theory (after Huston 1979), the repercussions of changes to woodlands since European settlement on birds and other animals can be inferred and compared directly with observed patterns.

Examining the group of birds considered to have declined, 25 of the 26 species are at least partly insectivorous and 17 species feed primarily on the ground (Table 1). As well as ground-foragers, this hypothesis also relates to bird species that take insects from the air and bark (noting that many of these insects have litter- and soil-dwelling larvae). In addition to reduced abundance, the productivity-based hypothesis suggests that arthropods and other invertebrate prey have become available over increasingly shorter periods, with reductions in the structural complexity of soil-rendering soil biota more vulnerable to short-term climatic variation (Bardgett 2005; Taylor 2008). Total biomass of invertebrates need not have decreased: it is the composition of invertebrate communities and their accessibility that is critical. Specifically, those larger taxa high in nutritional quality and found in the litter and topsoil (including beetles and their larvae, spiders and moth larvae) are considered most important in driving patterns of insectivore occurrence.

Quantifying variation in the abundance of these invertebrates is one way to test the productivity-based hypothesis directly (Usher *et al.* 1993; Recher *et al.* 1996). There have been several studies of litter and soil-dwelling invertebrates that conform to the hypothesis, reporting negative associations with grazing pressure (King and Hutchinson 1983) and fragment area (Zanette *et al.* 2000), and positive relationships with soil-moisture content and depth of litter (Noack 1996; Taylor 2008). In all of these studies, however, invertebrates were considered in terms of size or mass, rather than palatability or nutritional quality. Dietary information is available for many woodland insectivores – gut contents data (Lea and Gray 1935; Barker and Vestjens 1990) and selected foraging observations (e.g. Antos and Bennett 2006) – but I am unaware of any study that has used this information to estimate availability of likely prey (as opposed to total number of invertebrates or overall biomass).

Regional differences are consistent with the productivity-based hypothesis of woodland bird declines, whereby such declines are more marked in the winter rainfall regions in southern Australia (Reid 1999; Ford *et al.* 2001). The combination of hot and dry conditions in late spring–summer render these southern woodlands especially reliant on soil moisture, leading to inherently shorter growing seasons than in summer and summer-dominant rainfall regions further north (Mack 1989; McIntyre *et al.* 2002). Without additional moisture from rainfall, soil biota retreat to deeper strata or enter quiescent stages to survive, or both (Noack 1996). This annual pattern is likely compounded by climatic fluctuations associated with the El Niño Southern Oscillation and drought, further desiccating soils and reducing

availability of soil and litter-dwelling prey. These climatic fluctuations are not new but, when imposed on a degraded ecosystem that has been reduced to a series of disjunct fragments surrounded by an inhospitable matrix, the likelihood of prey shortages increases, explaining the previously reported coincidence of local extinctions with drought (Reid 1999; Mac Nally *et al.* 2009). These local and regional losses are expected to be lower in irruptive and migratory species owing to the increased likelihood of secondary recolonisation, explaining why most declining species are year-round residents.

Differences between habitat types can also be explained in terms of productivity, whereby those woodlands dominated by eucalypts show the most pronounced declines in ground-feeding insectivores. These sclerophyllous trees retain their leaves for up to 4 years and, once abscised, the heavily lignified leaves can take 3 years or longer to decompose (Attiwill *et al.* 1996). This leads to very low rates of litter-fall and organic inputs compared with other habitat types (Keith 1997; Grigg and Mulligan 1999; March and Watson 2007) rendering these soils inherently sensitive to altered nutrient cycles (Heatwole and Lowman 1986), especially when the original understorey has been replaced by annuals (McIntyre and Lavorel 1994). Woodlands composed of acacias and casuarinas are doubly buffered against changes to nutrient inputs. Firstly, they have inherently higher rates of litter-fall, driving greater levels of organic matter in the soil (Wilson and Johnson 1989; Clarke and Allaway 1996). Secondly, their litter is higher in nitrogen and decomposes more rapidly than that of eucalypts, leading to more constant levels of nitrogen in the soil for the decomposer community regardless of understorey composition (O'Connell 1986; Attiwill and Leeper 1987; Facelli and Pickett 1991). Callitris woodlands are intermediate in terms of litter-fall and decomposition rate (Lacey 1973; Harris *et al.* 2003), often growing in greater densities than eucalypts (Harris *et al.* 2003).

It should be noted that differences in productivity between regions and habitats are confounded with numerous historical factors, including the degree (and timing) of habitat loss and land-use, and overall climate (Heatwole and Lowman 1986). Rather than supplanting or ignoring these differences, the productivity-based hypothesis allows these woodlands to be compared directly, explaining *why* they differ in carrying capacity and *how* they differ in their resilience to changed land-use.

In addition to explaining observed declines, the changes in productivity can also explain recorded increases in some species. Those species limited by water availability would be expected to have benefited from the shift in water storage from within the soil to surface impoundments. Of the 29 native land-bird species Reid (1999) considered as 'increaser' species, 10 are granivores and a further four use mud for construction of nests, all of which would benefit from greater access to standing water (James *et al.* 1999; Franklin *et al.* 2000). Another species to have increased, the White-plumed Honeyeater (*Lichenostomus penicillatus*), is closely tied to riparian vegetation and standing water (Higgins *et al.* 2001), hence the widespread installation of dams and stock troughs throughout southern Australia may have facilitated their range expansion and could explain their continued dominance in many fragmented landscapes.

Reduced water infiltration also has direct effects on the growth and phenology of plants (Heatwole and Lowman 1986; Close and

Davidson 2004), leading to a range of direct and indirect responses in dependent animals. Nectar production is closely related to soil-moisture content via plant vigour (Wilson 2002), so that the availability of nectar through space and time would be expected to have diminished, especially for mass-flowering eucalypts which represent one of the main nectar sources in many woodlands (House 1997). Rather than manifesting in reduced flowering events, many sclerophyllous plant groups reabsorb nectar (Nicolson 1995, and references therein) or exhibit 'dry flowering', whereby flowers are still produced, but insufficient water and carbohydrates are available to produce nectar (House 1997). Increased incidence of dry flowering and increased variability of nectar availability through space and time may underlie recorded declines in Regent Honeyeaters (*Anthochaera phrygia*), Swift Parrots (*Lathamus discolor*) and Little Lorikeets (*Glossopsitta pusilla*) possibly extending to the ecologically similar Little Red Flying Fox (*Pteropus scapularis*). It is worth noting that all four species are highly dispersive (labelled 'rich patch fugitives' by Ford 2011), with movements of entire populations coinciding with mass flowering events of eucalypts (Franklin *et al.* 1989; House 1997). When coupled with large-scale land clearing, changes in nectar availability at regional scales may have disrupted movement patterns and changed long-term migratory routes.

The increased abundance of mistletoe and various root-parasitic shrubs (*Exocarpos* spp., *Leptomeria* spp.) in many remnant woodlands in eastern Australia is also consistent with the productivity-based hypothesis, with changes to nutrient inputs and water flows favouring these parasitic plants, especially along roadsides and other fragment edges. Providing reliable nectar, high-quality fruit, enriched litter and dense micro-habitats used by many species for nesting and roosting, these plants have a positive effect on many woodland species (Watson 2001; Bowen *et al.* 2009; Montague-Drake *et al.* 2009) having dramatic effects on the organic inputs and productivity of eucalypt woodlands (March and Watson 2007; Watson 2009). The positive response of these native plants to habitat degradation may mask the net effects of habitat fragmentation and agricultural intensification on woodland biota, effectively offsetting background reductions in food availability and habitat structure (Watson 2002). Given their parasitic habit, however, the high densities of mistletoes and root parasites in many woodlands represent an additional stressor on trees, and can contribute to increased mortality in severe cases.

### Predictions

The hallmark of any meaningful hypothesis is its ability to generate specific falsifiable predictions. The hypothesis developed herein is centred on changes in soil properties over time, but the historical data required to test this hypothesis critically are not available (Noble *et al.* 2007). Instead, using the space for time substitution that is commonplace in studies of habitat fragmentation and land-use, a series of comparisons can be made between contemporary woodlands. Importantly, these comparisons must be stratified within natural productivity gradients (e.g. Prober *et al.* 2002) – i.e. ridge-tops will always be less productive than valley floors. To guide these comparisons and enable further research to test, refute or refine the hypothesis, I articulate six

predictions. Five of these relate directly to the availability of soil- and litter-dwelling invertebrate prey, by which I mean those invertebrates that are both consumed by and accessible to insectivorous birds, not simply invertebrate abundance (see Hutto 1990 for a detailed exploration of this distinction and Fretz 2002 for an illustrative example).

- (1) There is a direct relationship between soil compaction (negative) and water infiltration (positive) on abundance of soil- and litter-dwelling invertebrate prey, mediated via altered functional diversity and biological activity of soil microbial communities.
- (2) There are more active microbial communities and more available soil- and litter-dwelling invertebrate prey in callitris woodlands than eucalyptus woodlands, more in acacia and casuarina–allocasuarina woodlands than callitris woodlands, and more in woodlands in summer-dominant rainfall regions than otherwise similar woodlands in winter-dominant rainfall regions owing to summer drought stress.
- (3) Abundance, species richness and reproductive output of woodland birds are greater in sites with greater availability of invertebrate prey.
- (4) Individual ground-foraging insectivores display poorer body condition and higher stress levels in sites with shallower litter and topsoil, especially in summer.
- (5) Woodland bird assemblages display lower species turnover (within and between years) in sites with deeper litter owing to less seasonal variation in available soil- and litter-dwelling invertebrate prey.
- (6) Other taxa that feed on the same litter- and soil-dwelling invertebrates (e.g. dasyurid marsupials, molossid bats, agamid lizards) exhibit similar declines to declining woodland birds in both extent and severity.

### Prospect

Rather than an idiosyncratic response of a small number of species, declines in woodland birds are symptomatic of a far wider malaise – the widespread and ongoing degradation of remaining woodlands in southern Australia (Recher 1999). With decreasing numbers of hollows, increased spread of exotic predators and incremental loss of remaining habitat, many native species are undergoing unprecedented declines and entire guilds are facing local extinction (Ford *et al.* 2001; Mac Nally *et al.* 2009). Considering these patterns in terms of productivity complements existing landscape and historical approaches and may provide a useful lens to clarify other unanswered questions. Hence, having considered patterns of occurrence of woodland birds to be influenced by availability of their favoured prey, how have declining numbers of woodland birds affected avian predators? Might reductions in ground-foraging insectivores underlie marked declines in various ground-dwelling predators, such as Common Death Adders (*Acanthophis antarcticus*)? Have reductions in the abundance of woodland birds (especially larger bodied nectarivores and insectivores) led to reduced numbers of bird-feeding raptors including Square-tailed Kites (*Lophoictinia isura*) and Barking Owls (*Ninox connivens*)? As well as higher trophic levels, the productivity-based hypothesis also has relevance for plants and their animal associates. In addition to

lowering the standing crop of nectar, has the degradation of woodland soils made woodland plants more susceptible to herbivores and other natural enemies? Could increases in water stress have made trees more prone to attack by psyllids (see Heatwole and Lowman 1986), potentially boosting the resource-base for foliage gleaning species like Noisy Miners (*Manorina melanoccephala*), Striated Pardalotes (*Pardalotus striatus*) and Weebills (*Smicrornis brevirostris*)? Moving beyond southern Australia, might similar reductions in food resources explain declines in forest, woodland and farmland birds elsewhere, underlying reported responses to fragment size (Robinson 1998), habitat structure (Fuller *et al.* 2007) and agricultural intensification (Donald *et al.* 2001)? These open questions exemplify the value of a resource-based approach, allowing researchers to move beyond describing patterns to ask specific testable questions and address underlying processes.

The single most important implication of the productivity-based hypothesis is the realisation that not all woodlands are the same. Woodland on a stony ridge and woodland on a floodplain provide very different resources for plants and animals, and exhibit very different fluctuations in resource availability through time – the soils that grow more wheat and wool originally grew more robins and babblers. As well as having dramatic effects on their dependent fauna, the issue of representation also affects the perceptions of landholders, conservation managers and policy makers. Woodlands are widely regarded as inherently rocky, restricted to poor soils and lacking in structure. Although this may describe most woodlands remaining, the perception that this is the standard must be challenged. Woodlands can be productive, woodlands thrive on fertile soils, woodlands can have complex ground layers. As pressures from expanding cities and intensifying agriculture continue, we must be increasingly shrewd in determining which areas can be sacrificed, and which must be retained. Offsets for development are becoming commonplace and investment in large-scale restoration is expanding. Those remaining woodlands on deeper and more productive soils must be preserved, and revegetation efforts must concentrate on these lowland parts of catchments.

## Acknowledgements

The ideas expressed here were crystallised during Birds Australia's Conservation Forum in Bendigo, and I thank my fellow speakers for sharing their insight. I am indebted to Ian Lunt for responding to my persistent questions about nutrients and water, and to Veronica Doerr, Hugh Ford, Martine Maron, Maggie Watson, Michael Watson and two anonymous referees for their considered input and suggestions on earlier drafts.

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Manuscript received 27 November 2009, accepted 15 April 2010